Interference of *Choricarpia leptopetala* by *Lantana camara* with nutrient enrichment in mesic forests on the Central Coast of NSW

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Abstract

Suppression of *Choricarpia leptopetala* (F. Muell.) Domin., an early native coloniser of mesic forests, by *Lantana camara* L. was evaluated using field-based variable density and substitution experiments. Sites were located in disturbed areas within wet sclerophyll forest and warm temperate rainforest near Lake Macquarie on the Central Coast of NSW. In the variable density experiment, *C. leptopetala* growth was significantly suppressed by 36.4% from 3.3 to 2.1 g plant⁻¹ in the presence of equal proportions of *L. camara* at a total density of 20 seedlings m⁻², only when nutrients (60 g m⁻² of a slow release NPKS fertiliser) were added to the soil surface. *Lantana camara* growth significantly increased by 14.6% from 4.1 to 4.7 g plant⁻¹ when nutrients were added. At a density of 40 seedlings m⁻², growth of *C. leptopetala* was suppressed by 37.5% from 3.2 to 2.0 g plant⁻¹ in the zero nutrient treatment with equal proportions of *L. camara*, and was further suppressed by 40.0% from 2.0 to 1.2 g plant⁻¹ with the addition of nutrients. *Lantana camara* growth significantly increased by 43.7% from 2.3 to 3.3 g plant⁻¹ when nutrients were added. Pure stands of *C. leptopetala* did not respond significantly to nutrient addition at either density. In the substitution experiment (with a constant density of 20 seedlings m⁻²), *C. leptopetala* growth was significantly suppressed by 44.1% from 3.4 to 1.9 g plant⁻¹ when *L. camara* reached 75% of stand composition in the zero nutrient treatment and by 43.2% from 3.7 to 2.1 g plant⁻¹ when it reached 50% of stand composition in the nutrient addition treatment.

The results link interference and suppression of native colonisers by exotic invaders with demonstrated increases in resource availability following ecosystem disturbance. *Lantana camara* is able to take better advantage of increased resource availability than *C. leptopetala*, thereby accumulating more biomass and suppressing the growth of *C. leptopetala*. Suppression of *C. leptopetala* also increased when the density of *L. camara* was increased. Consequently, the negative effect of the invading species on the indigenous species is both nutrient-addition and density dependent. Models describing interference in ecosystem recovery following disturbance need to include interference processes associated with weed invasion that disadvantage indigenous species.

Nomenclature: Harden (1990).

Introduction

The invasion of exotic plants into natural communities is widespread and has been identified as a threat to global biodiversity (Radosevich & Holt 1984; Binggeli 1996). Within Australia, many exotic species have become long-term and sometimes dominant components of important communities (Re-

jmanek 1989; Swarbrick et al. 1995). Disturbances such as altered fire regimes, structural damage, and increased urban run-off are often implicated when the invasive species becomes established and gains dominance. Gentle & Duggin (1997a) showed that the invasion of the thicket-forming shrub *Lantana camara* L. significantly increased following disturbances associated with fire or grazing. Invasion was more successful

with increasing intensity of disturbance, principally because disturbance increased resource availability such as light and nutrients (Duggin & Gentle 1998). *Lantana camara* utilises these resources to advantage by rapidly growing and occupying the site. In addition to occupying the site, *L. camara* may also interfere with regeneration and growth of native forest colonisers by interspecific competition for resources and/or allelopathy. The impact of exotic invaders on suppression of early colonising native species following disturbances has rarely been tested and needs to be evaluated.

The aim of this study was to experimentally measure the interference between neighbouring seedlings of *Choricarpia leptopetala* (F. Muell.) Domin., an early native coloniser of mesic forests, and *L. camara* in disturbed patches of wet sclerophyll forest and warm temperate rainforest, and whether the level of interference was influenced by nutrient availability. Suppression of one species by the other may result from interspecific competition for soil-based resources through resource monopolisation, greater utilisation efficiency, allelopathy, or any combination of these processes. The experimental designs assumed that unequal sharing of resources between species growing in a mixture would affect seedling growth. The experiments were not intended to distinguish processes in resource sharing and interference, but to measure the growth response of *C. leptopetala* seedlings to the invasion of *L. camara* in disturbed and nutrient enriched forest communities. Consequently, the null hypothesis is that increased nutrient availability and seedling density of *L. camara* does not lead to higher levels of suppression of *C. leptopetala*.

Invasion by exotic species has a significant impact on the structure, floristics, and functioning of natural ecosystems (e.g., Lamb 1982; Bhatt et al. 1994). Impacts can be initiated at the establishment phase following disturbance and through all stages of stand development. Results from interference experiments such as these will provide an understanding of how such interactions might affect the regeneration and survival of native colonising species and, therefore, the long-term viability of communities. *Lantana camara* is one species that is likely to produce such changes when invading wet sclerophyll forest and warm temperate rainforest and shift community composition and structure to the long-term detriment of community integrity.

Methods

The experimental sites were located in wet sclerophyll forest and warm temperate rainforest situated west of Lake Macquarie (33°03' S and 151°22' E) on the Central Coast of New South Wales, Australia (Gentle & Duggin 1997b). Altitude varied from 45 to 260 m a.s.l. across the area and rainfall (mean 1198 mm yr⁻¹) is distributed relatively evenly throughout the year, although a peak occurs during February/March. The measured mean monthly maximum temperature for the experimental period varied from 26.5 °C (January) to 15.8 °C (June) and the minimum from 16.9 °C (January) to 6.0 °C (July). The soils are podzolics with a sandy clay loam A horizon over a light to medium clay.

The wet sclerophyll forest is dominated by *Eucalyptus pilularis*, *E. saligna* and *Syncarpia glomulifera* in the main canopy with *Allocasuarina torulosa*, *Acacia longifolia* and *A. melanoxylon* forming a secondary upper stratum. The warm temperate rainforest includes the canopy species *Ceratopetalum apetalum*, *Doryphora sassafras*, *Schizomeria ovata*, *Elaeocarpus reticulatus*, *Glochidion ferdinandi*, and *Endiandra sieberi*. Small trees and tall shrubs included *Callicoma serratifolia*, *Backhousia myrtifolia*, *Acmena smithii*, *Choricarpia leptopetala*, *Pittosporum undulatum*, and *Cryptocarya rigida*. The most common indigenous climbers in both communities included *Geitenoplesium cymosum*, *Dioscorea transversa*, *Parsonsia straminea* and *Cissus hypoglauca*.

Two experiments were established in forests that have been disturbed through localised vegetation removal, altered fire regimes, trampling, and local urban run-off. The first experiment was a variable density experiment with *L. camara* and *C. leptopetala* seedlings in combined densities of 20 or 40 plants m⁻². The second was a substitution experiment with *L. camara* and *C. leptopetala* seedlings fixed at a constant density of 20 plants m⁻². Each experiment was established as a complete factorial arrangement with three factors: (i) seedling density (D) or species replacement (R), (ii) nutrient addition (N), and (iii) forest community (F) in four blocks comprising twelve 3 × 3 m plots each. Two blocks were established in wet sclerophyll forest and two in warm temperate rainforest. Areas of existing canopy disturbance were utilised, with any ground cover, including litter, removed prior to establishing the experiment. The cleared area extended at least 3 m from all sides of each block. A buffer zone of 0.5 m separated each plot.

The variable density experiment used four seedling densities: 10 seedlings m^{-2} of each species to give a total density of 20 seedlings m^{-2} in a mixed stand; 20 seedlings m^{-2} of *C. leptopetala* in a pure stand; 20 seedlings m^{-2} of each species giving a total of 40 seedlings m^{-2} ; and 40 seedlings m^{-2} of *C. leptopetala* in a pure stand. The two nutrient addition levels were: zero nutrient treatment; and surface soil fertilised with 60 g m^{-2} of slow release fertiliser (Osmocote) containing 18% N (as 7.5% NO_3 and 10.5% NH_4); 4.8% P (as PO_4), and 8.3% K and 3.0% S (as K_2SO_4). Nutrients were applied as dry granules and were mixed through the upper 10 cm of surface soil. A slow release fertiliser was used to avoid a shift in the species interaction from competition for nutrients to that for light (Keddy 1989).

The substitution experiment with constant density (20 seedlings m^{-2}) used four substitution levels: 20 seedlings m^{-2} of *C. leptopetala* in a pure stand; 15 seedlings m^{-2} of *C. leptopetala* with 5 seedlings m^{-2} of *L. camara*; 10 seedlings m^{-2} of *C. leptopetala* with 10 seedlings m^{-2} of *L. camara*; and 5 seedlings m^{-2} of *C. leptopetala* with 15 seedlings m^{-2} of *L. camara*. The nutrient addition levels were the same as those used in the first experiment.

The following environmental variables were measured within each plot as indicators of initial conditions and within-block homogeneity: (i) soil pH, electrical conductivity (EC) and temperature at 5 cm depth, and (ii) soil seed bank and seed rain of *L. camara* and *C. leptopetala*. Duplicate soil samples were taken from the upper 10 cm of mineral soil using a 7 cm diameter corer, with samples obtained from three random locations within each plot. Soil pH was determined using a 'Checker' pH Meter (Hanna Instruments) with a 1:5 soil:water suspension. Soil EC was similarly measured with a TPS LC 84 Conductivity Meter (TPS Pty Ltd, Brisbane). The soil seed bank was determined from a composite soil sample collected from the upper 5 cm by sieving, separation by flotation, and hand sorting (Roberts 1981). Seed rain was measured over the experimental period by placing one trap within each plot (with a catchment area of 30 × 30 cm at 1 m above ground). These consisted of filter paper covered by a non-drying glue (Konishi Bond, Konishi Co Ltd, Japan) within gauze frames. Five seed traps were destroyed during the experimental period and the data were treated as missing observations in the analysis.

Seeds of both species were obtained from the vicinity of each block during August, 1993. The

seeds were soaked for 18 hr prior to sowing in September 1993. Seedling densities were established by sowing 100 seeds of each species uniformly within 1 m^2 central subplots and covering to a depth of 1 cm. Seedlings were thinned 12 weeks after sowing to the required density and composition for each plot, maintaining an even distribution of species within the mixed stands. Seedlings that died within the first three months were replaced from a spare plot.

Soil EC, as an indicator of soil fertility, was again measured 14 months after nutrient addition (November, 1994) to determine changes resulting from the addition of the slow release fertiliser.

Seedling numbers were recorded twelve months after sowing, and again at 18 months when all seedlings were harvested (March 1995). Some seedling mortality occurred towards the end of the experiment, principally due to dry conditions during late summer and early autumn (January-March 1995). All plant material (above and below ground) was harvested, separated by species, washed, dried at 70 °C for 48 h, and weighed.

Seedling biomass data were ln transformed for ANOVA after significant heteroscedasticity was found using the maximum F ratio test and a Shapiro-Wilk analysis. Where the F test for treatments in the analysis of variance was significant ($P < 0.05$), the significance of the differences in means was assessed using LSD procedures (Burr 1981). Environmental variables were compared between plots, before and after treatment application, using one and two-way ANOVA.

Results

Distribution of propagules

Seed rain for *C. leptopetala* and *L. camara* was not significantly different between the wet sclerophyll forest and the warm temperate rainforest (Table 1). Seed banks for both species (Table 1) were significantly higher in the wet sclerophyll forest than the warm temperate rainforest ($P < 0.05$ for *C. leptopetala* and $P < 0.01$ for *L. camara*). Consequently, the presence of propagules of both species in disturbed patches in both forest communities suggests that the interaction between them is likely to be ecologically important.

Table 1. Seed rain (seeds $\text{m}^{-2} \text{yr}^{-1}$) and seed bank (seeds m^{-2}) for *C. leptopetala* and *L. camara* in wet sclerophyll forest and warm temperate rainforest for the study area near Lake Macquarie, NSW.

Species and seed source	Wet sclerophyll forest	Warm temperate rainforest	Significance
<i>C. leptopetala</i>			
Seed rain	1.24	1.75	ns
Seed bank	1.84	1.08	*
<i>L. camara</i>			
Seed rain	2.23	1.96	ns
Seed bank	2.38	1.35	**

ns = not significant; * = $P < 0.05$; ** = $P < 0.01$.

Soil fertility

Soil EC, as an indicator of soil fertility, was significantly lower ($P < 0.001$ for the one-way ANOVA of forest communities) in the wet sclerophyll forest (0.118 dS m^{-1}) than the warm temperate rainforest (0.121 dS m^{-1}) before the commencement of the experiment. The addition of nutrients significantly increased soil EC when measured 14 months after treatment application ($P < 0.05$ for the two way ANOVA of forest communities and nutrient addition). Soil EC rose by 7.6% in the wet sclerophyll forest to 0.127 dS m^{-1} , and by 5.8% in the warm temperate rainforest to 0.128 dS m^{-1} . The difference between forest communities was not significant 14 months after nutrient addition.

Forest communities

The response of *C. leptopetala* and *L. camara*, as measured by biomass production, was not significantly different for the wet sclerophyll forest and warm temperate rainforest for both experiments, either as a main effect or in lower order interactions. All seedling response results, therefore, have been presented as mean values across forest communities. Biomass production for *C. leptopetala*, however, tended to be consistently higher, but not significantly so, in wet sclerophyll forest than in the warm temperate rainforest, particularly when nutrient additions were made to pure stands of that species or in stands with low densities of *L. camara* (25% or less).

Figure 1. Mean seedling biomass (g plant^{-1}) of *C. leptopetala* growing in the variable density experiment using two seedling densities (20 and 40 plants m^{-2}), either in mixed or pure stands, and with or without nutrient addition.

Variable density experiment

Seedling growth of *C. leptopetala* (Figure 1) in mixed stands at 20 seedlings m^{-2} was not significantly suppressed when compared with pure stands at the same density (3.3 compared with 3.4 g plant^{-1}). However, growth was significantly suppressed ($P < 0.01$) when nutrients were added to mixed stands (36.4% reduction from 3.3 to 2.1 g plant^{-1}), while growth in pure stands did not significantly increase with the addition of nutrients (3.4 compared with 3.7 g plant^{-1}). Conversely, total *L. camara* growth significantly increased by 39.8% from 28.4 to 39.7 g m^{-2} in mixed stands ($P < 0.001$) with the addition of nutrients (Table 2).

The growth of individual *C. leptopetala* seedlings (Figure 1) in mixed stands at 40 seedlings m^{-2} was significantly suppressed (37.5%) compared with pure stands at the same density (2.0 compared with 3.2 g plant^{-1}). The addition of nutrients further suppressed growth significantly in mixed stands (40.0% reduction from 2.0 to 1.2 g plant^{-1}) but not in pure stands (3.2 compared with 3.0 g plant^{-1}). Again total *L. camara* growth significantly increased by 47.5% from 37.9 to 55.9 g m^{-2} in mixed stands with the addition of nutrients (Table 2).

Substitution experiment

Suppression of *C. leptopetala* at 50% *L. camara* composition (10:10) in the zero nutrient treatment (Table 3) was not significant at 2.9% of the pure stand (3.3

Table 2. Mean plot biomass (g m^{-2}) for *C. leptopetala*, *L. camara*, and total biomass growing at two densities (20 and 40 plants m^{-2}), either in mixed stands of equal proportions or as pure stands of *C. leptopetala*, and with or without nutrient addition (0 or 60 g m^{-2} of a slow release NPKS fertiliser).

Seedling density (plants m ⁻²)	Plot composition	Nutrient addition (g m ⁻²)	<i>C. leptopetala</i>	<i>L. camara</i>	Total
20	Mixed stand	0	28.3	28.4	56.7
		60	16.2	39.7	55.9
	Pure <i>C. leptopetala</i>	0	62.6	0.0	62.6
		60	64.0	0.0	64.0
40	Mixed stand	0	20.2	37.9	58.1
		60	11.2	55.9	67.1
	Pure <i>C. leptopetala</i>	0	108.7	0.0	108.7
		60	101.6	0.0	101.6
Significance			*	***	*
LSD _(0.05)			11.3	4.2	16.2

* = $P < 0.05$; *** = $P < 0.001$.

Table 3. Mean seedling biomass (g plant^{-1}) for *C. leptopetala* and *L. camara* growing in the substitution experiment with a constant density of 20 seedlings m^{-2} , with or without nutrient addition (0 or 60 g m^{-2} of a slow release NPKS fertiliser). LSD_(0.05) for *C. leptopetala* = 0.64 and *L. camara* = 0.32.

Nutrient addition (g m^{-2})	Species composition					Significance
	<i>C. leptopetala</i>	20	15	10	5	
	<i>L. camara</i>	0	5	10	15	
0	<i>C. leptopetala</i>	3.4	3.2	3.3	1.9	**
	<i>L. camara</i>	0.0	5.2	4.1	3.7	***
60	<i>C. leptopetala</i>	3.7	3.1	2.1	1.2	**
	<i>L. camara</i>	0.0	6.2	4.7	4.9	***

** = $P < 0.01$; *** = $P < 0.001$.

compared with 3.4 g plant^{-1}) whereas suppression was significant ($P < 0.05$) at 43.2% for the nutrient added treatment (2.1 compared with 3.7 g plant^{-1}). At 75% composition (5:15) suppression was significant at 44.1% (1.9 compared with 3.4 g plant^{-1}) and 67.6% (1.2 compared with 3.7 g plant^{-1}) for the zero and nutrients added treatments respectively. Suppression was more pronounced when nutrients were added and came into effect at lower densities of *L. camara*. Suppression was also evident in the zero nutrient treatments but only when *L. camara* occurred in higher proportions in the stand.

Seedling growth of *C. leptopetala* was not significantly affected by the addition of nutrients to pure

stands of that species and in stands where *L. camara* comprised 25% of stand composition (15:5, Table 3). *Lantana camara* had significantly greater biomass per plant ($P < 0.001$) when nutrients were added across all combinations of species composition used.

Total biomass production in the zero nutrient treatment (Figure 2a) steadily declined with increasing proportions of *L. camara* but the difference was only significant ($P < 0.05$) between the pure stands of *C. leptopetala* (20:0, 62.6 g m^{-2}) and where *L. camara* comprised 75% of the stand (5:15, 46.5 g m^{-2}). The other combinations were not significantly different from each other and from the previously mentioned species combinations. Total biomass production for the nutrient addition treatment (Figure 2b) was not significantly different across the species composition range and was similar to the zero nutrient treatment (Figure 2a), except where *L. camara* composition was 75% (69.8 compared with 46.5 g m^{-2} , $P < 0.05$). However, the proportional contribution to total biomass production by *L. camara* was significantly higher ($P < 0.001$) across the entire species combination range when nutrients were added (Figure 2b compared with Figure 2a) increasing from 31.5% when *L. camara* composition was 25% of the stand to 59.2% when it was 75% of the stand. Conversely, biomass production by *C. leptopetala* significantly decreased ($P < 0.05$) when *L. camara* composition was 50% when nutrients were added.

Figure 2. Mean plot biomass (g m^{-2}) of *C. leptopetala* (C.l., ●-●) and *L. camara* (L.c., ○-○) and total biomass (■-■) in the substitution experiment using different species mixes under constant plant densities (20 seedlings m^{-2}), with (b) or without (a) nutrient addition. $\text{LSD}_{(0.05)}$ for *C. leptopetala* = 9.8, *L. camara* = 4.0 and total biomass = 14.0.

Discussion

Propagules of both *C. leptopetala* and *L. camara* occur as seed rain and in the seed bank of disturbed patches in wet sclerophyll and warm temperate rainforest on the central coast of NSW. *Choricarpia leptopetala* is an indigenous colonising and riparian species commonly found in disturbed areas used in these experiments. Areas supporting *C. leptopetala* are characterised by more fertile sites with higher water availability, such as gullies in wet sclerophyll forest, margins of rainforest patches and disturbed sites. Both *C. leptopetala* and *L. camara* regenerate from dispersed seed and seed banks in these environments. Consequently, their occurrence suggests that interference between the early native coloniser and the exotic weed is likely to be an important ecological issue in relation to community recovery following disturbance.

Increased soil fertility significantly increased the suppression of *C. leptopetala* by *L. camara* in both forest communities. Likewise, increasing the density of *L. camara* increased the suppression of *C. leptopetala*. Consequently, the negative effect of *L. camara* on the native species is both nutrient-addition and density dependent. Interference mechanisms were not intended to be identified from the experimental design, although a relationship between the degree of suppression and the level of macronutrient availability is evident. Initial suppression allows greater differences in seedling growth rates which, in turn, permits other forms of 'aggressive' competition associated with resource utilisation and allelopathy to be invoked. Such processes

will promote long-term persistence of the invading species.

The results concur with several models established to describe processes associated with resource competition and plant invasions by identifying impacts of invasive populations on the dynamics of disturbed plant communities (e.g., Miller 1967; Trenbath 1974; Silander & Antonovics 1982; Tilman 1987; Wilson 1988). Importantly, the ability of invasive species to suppress neighbours is influenced by the level of availability of soil-based resources. Growth characteristics and shallow rooting of *L. camara* have been attributed to the success of the species in taking advantage of increased nutrient availability within the surface soil and, therefore, its ability to compete more effectively in areas of soil disturbance (Hobbs 1989; Swarbrick et al. 1995). Our results show that *L. camara* is able to suppress at least one indigenous species adapted to regenerating within disturbed areas. Other indigenous colonising species need to be tested in similar sets of experiments to those described to reveal any differences among species in their susceptibility to interference by invading *L. camara*. In this way the community response to invasion can be evaluated.

Population persistence after invasion has been attributed to frequent disturbance, structural changes, or actual changes in ecosystem functioning caused by invasive populations (Lamb 1982; Fensham et al. 1994; Rawat et al. 1994). The results presented here suggest that population persistence and thicket formation is also possible by a species interfering with the growth and development of another. Competitive ability may

be increased by changes in nutrient levels following soil disturbance, nutrient releases and understorey damage following fire, increased light through forest canopy damage, and reduced neighbour competition. In the case of rainforest communities, any process that prevents the re-establishment of the typical micro-environment, such as the establishment of persistent monospecific thickets, will enhance the chances of persistence of invasive populations (Hobbs & Huenneke 1992; Brown 1994). Any mesomorphic species capable of germinating and growing under low irradiance would be favoured, although competition for soil-based resources will remain an important influence on relative success. Eucalypt seedlings, on the other hand, are less capable of germinating, surviving and growing under conditions of low irradiance within thickets, in comparison to more mesomorphic species. This has implications for community dynamics particularly where populations of *L. camara* establish in wet sclerophyll eucalypt forests and rainforest-eucalypt forest ecotones.

The findings of this study show the importance of increased nutrient availability and the density of *L. camara* in restricting the growth of a native coloniser. Clearly, management practices must avoid significant increases in surface-soil nutrient availability in areas prone to *L. camara* invasion, particularly when canopy damage occurs. Successful management will require a thorough knowledge of the impacts of *L. camara* on indigenous species and community dynamics so that ecosystem integrity can be maintained.

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